ROOT ANATOMY OF THREE CARNIVOROUS PLANT SPECIES

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Introduction

The majority of terrestrial carnivorous plants grow in organic soils in bogs and fens, in which they encounter persistent unfavourable conditions. The soils are usually wet or waterlogged, mostly acid, usually poor in available mineral nutrients, and can contain phytotoxins (Juniper *et al.*, 1989). Generally, carnivory in most terrestrial plants may be considered as an adaptation to all of these stress factors (Adamec, 1997). Many carnivorous plant species take up the majority of N, P, K, Ca, and Mg for their growth by roots from mineral-poor wet soils but a weakly developed root system is a common characteristic for most species (Adamec, 1997, 2002). Roots are usually short and weakly branched. Nevertheless, knowledge of anatomical structure for carnivorous plant roots is very low and unsufficient (Guttenberg, 1968; Kutschera & Sobotik, 1992a,b). Recently, items of knowledge of carnivorous plant roots have been compiled by Adlassnig *et al.* (2005). Carnivorous plants grow with many non-carnivorous wetland plant species, mostly graminoids and cyperoids, which are characterized by a marked anatomical adaptation of their roots and rhizomes to soil anoxia which is based on development of voluminous air spaces in roots or rhizomes (Justin & Armstrong, 1987).

The aim of this paper is to present basic anatomical structure of roots of three terrestrial carnivorous plant species, *Dionaea muscipula*, *Drosera adelae*, and *Sarracenia rubra*, and to discuss whether the anatomical structure of their roots is related rather to carnivory or to an adaptation to soil anoxia.

Materials and Methods

All plant material was collected from a naturally lit greenhouse collection of carnivorous plants during June-July. The plants used were propagated vegetatively by dividing adult plants. They were grown in 10 × 10 × 10cm plastic pots in natural organic soils (Adamec, 2002). *Drosera adelae* F.Muell. (native to northeast Australia) was grown in a mixture of an acidic fen soil and perlite (approximately 6:1 ratio by volume), while *Dionaea muscipula* Ell. and *Sarracenia rubra* Walt. (both native to the southeast USA) were both grown in a mixture of conifer needle mould with vermiculite (approximately 4:1 ratio by volume; for the details see Adamec, 2002). The pots with the plants were placed in a 0.8m^2 white polypropylene container 0.4m high, filled with rainwater to a depth of 2-3cm.

One typical adventitious root was excised for each of three adult plants of each species. The length of the excised roots ranged within 3.8-6.5cm in *Drosera adelae*, 3.5-4.0cm in *Dionaea muscipula*, and 7.2-11.0cm in *Sarracenia rubra*. The roots were shaken thoroughly in tap water to remove soil particles. They were fixed with a 70% FAA solution[1]. Three-mm long segments of root tips, middle parts, and bases were embedded into paraffin. Ten-µm thick sections of root tips, and 15-µm sections of the other root segments, were cut using a microtome. The preparations were stained by 0.1% Alcian Blue (Alcianblau 8 GS, Fluka, FRG) in 3% acetic acid for 2 hours. Then they were stained by 0.1% Safranine (Safranine T, Fluka) in citrate-phosphate buffer (pH 4.0) for approximately 16 hours. Parallel preparations were tested for lignin by histochemical staining by 1% Phloroglucinol (Phloroglucinol, Fluka) in ethanol with HCl. All preparations were mounted to Solacryle (Solakryl, Synthesia, Kolín, Czech Republic). The proportion of air spaces to root cross-section area was estimated by scanning the photographs of cross-sections in which the air spaces had been blackened by hand. The proportion of central cylinder to the total root cross-section area was calculated from diameters of central cylinder and the root.

[1]A mixture of 5 ml 40% formaldehyde, 90 ml 70% ethanol, and 5 ml glacial acetic acid.

The Safranine stains provided unsatisfactory results. This method stains lignified xylem elements, and since parallel stains prepared using Phloroglucinol+HCl (a classical test for lignin) also demonstrated only weak staining, we conclude that the xylem elements in carnivorous plant roots contain a very low content of lignin. However, additional tests (Mäule reaction, aniline sulphate test) should be used to support this conclusion.

The anatomical structure in differentiated middle parts of carnivorous plant roots was the same as that in basal root parts. Root hairs were present in all three species, but the occurrence of root hairs was variable among the species and single roots. On some images, root hairs were not visible (see Figures 1-4). Generally, the anatomical structures of Droseraceae roots (e.g. *Drosera adelae, Dionaea muscipula*; Figures 1, 2) were similar, and differed from that of *S. rubra* (see Figure 3). Roots of *Drosera adelae* and *Dionaea muscipula* (middle and basal parts) were covered with impregnated one-layer-celled rhizodermis which was only partly kept in *Dionaea*. Exodermis (external layer of cortical cells below rhizodermis with suberinized cell walls having a protective function) was developed only in *D. adelae* and *S. rubra* roots (Fig. 1, 3), but not in *Dionaea* roots (Fig. 2). This finding is in harmony with Guttenberg (1968) and Adlassnig *et al.* (2005). Cortex in roots of both Droseraceae species was relatively thin and contained smaller and larger intercellular spaces, but no voluminous air spaces. Natively colored (brown), thin-walled endodermis was also impregnated and, judging from its stainability by Safranine, it was lignified. Casparian strips (*i.e.*, impregnated parts of radial cell walls) were not detected clearly in the endodermis in roots of either zone. A relatively thick central cylindrical zone contained radially arranged vascular tissues, the phloem and xylem. In *Drosera adelae*, two phloem poles occurred atypically also in central part of the central cylinder (see Figure 4). While this arrangement of phloem poles is rare, may occur in Droseraceae roots (Guttenberg, 1968; A. Lux, pers. commun.).

The middle and basal parts of *S. rubra* roots were covered with an intensively impregnated thin rhizodermis (see Figure 3). In contrast with the cortex of the Droseraceae plants, the cortex in *S. rubra*

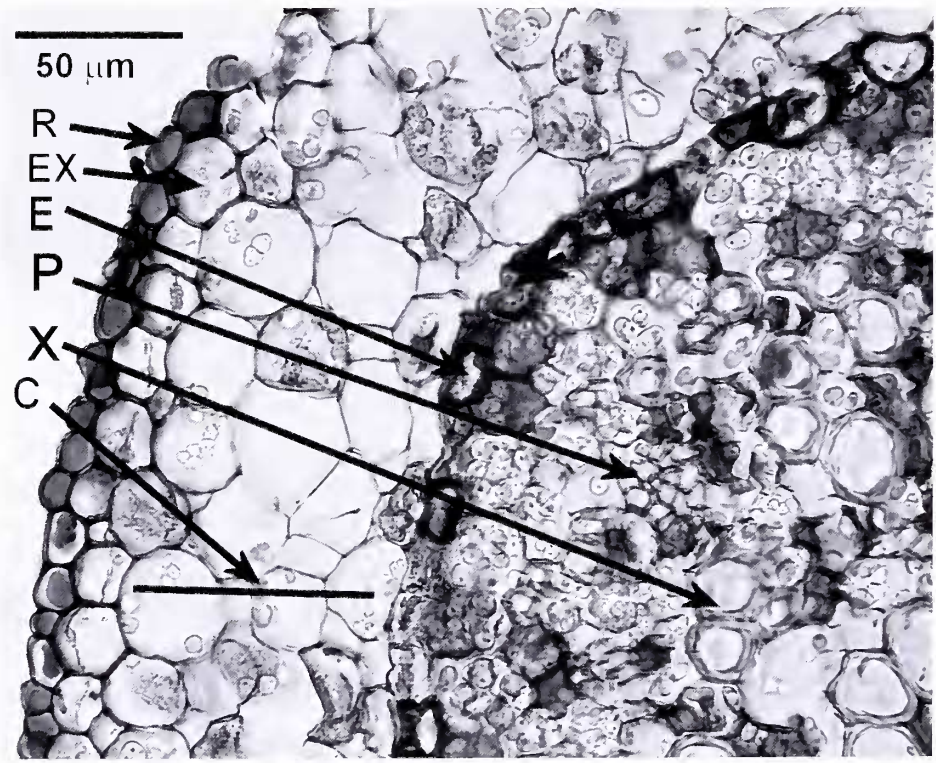

Figure 1: Cross-section through middle part of *Drosera adelae* root. The dark structures were stained by Safranine and Alcian Blue. R, rhizodermis; EX, exodermis; C, cortex; E, endodermis; P, phloem; X, xylem.

roots was distinctly subdivided into two zones. The external hypodermal zone consisted of three layers of small, natively colored (brown) cells, while the internal acrenchymatous zone was formed by a column-shaped cell arrangement around large air spaces. In some preparations, Casparian strips were present in the non-impregnated endodermis. The central cylinder contained a great proportion of sclerenchymatous tissues. Xylem poles were more distinct than phloem ones. Differentiated parts of roots of all three carnivorous plant species contained starch grains. The greatest starch content occurred in *Drosera adelae* roots (see Figure 1).

Generally, this study has revealed a considerable similarity of the root anatomy of carnivorous plants with that of other wetland non-carnivorous plants, especially dicot species (*e.g.*, Justin & Armstrong, 1987), and the degree of anatomical adaptation of carnivorous plant roots to soil anoxia may be discussed. The proportion of intercellular and air spaces within the differentiated roots could amount to approximately 5-10% of the total root cross section area in *Drosera adelae* and *Dionaea muscipula* (see Figures 1, 2), while approximately 20% in *S. rubra* (see Figure 3). These values are comparable with those of root porosity, estimated using a pycnometric method, reported by Justin & Armstrong (1987) for 42 wetland dicot and monocot plant species (usually to within 5-45%). Thus, carnivorous plants lie near a lower limit of root porosity in wetland plants. However, when information on the structure of carnivorous plant roots is combined with recent results on measurements of radial oxygen loss from carnivorous plant roots to anoxic medium (Adamec, 2005) two different strategies of oxygen economy within carnivorous plant roots may be suggested. Roots of Droseraceae with a low proportion of air spaces, prevent against radial losses of oxygen by an impregnated, impermeable rhizodermis or exodermis, and are able to conduct oxygen up to root tips. Meanwhile, in *Sarracenia* roots which have a greater proportion of air spaces, longitudinal diffusive oxygen fluxes are much greater, but a considerable part of oxygen leaks radially from the roots. As carnivorous plant roots grow under permanently anoxic soil conditions it is possible to conclude that roots of carnivorous plants are well adapted to living in anoxic soils and the aeration mechanism is sufficient to supply the whole roots with oxygen until the shoots are flooded.

Carnivorous plant roots do differ considerably from roots of wetland non-carnivorous plants in their

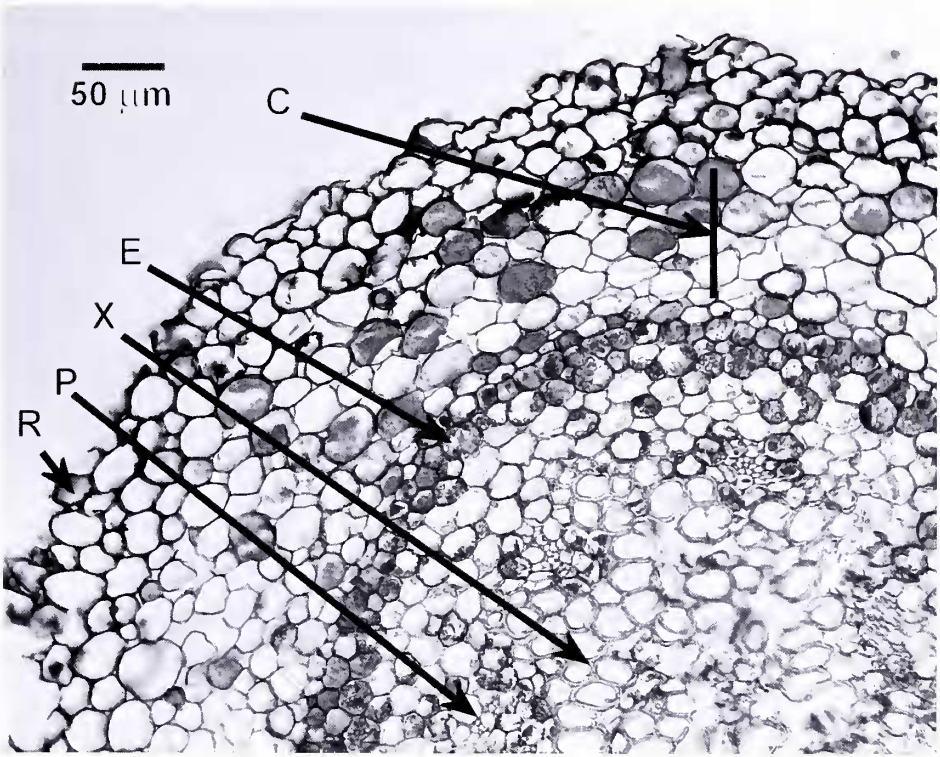

Figure 2: Cross-section through basal part of *Dionaea muscipula* root. R, rhizodermis; EX, exodermis; C, cortex; E, endodermis; P, phloem; X, xylem.

great proportion of central cylinder to the total root cross-section area. While the proportion in differentiated roots of several wetland non-carnivorous plant species was mostly within 3-8% and only exceptionally 34% (Justin & Armstrong, 1987), the proportion was much greater in all three carnivorous plant species investigated, i.e 46-48% in *Drosera adelae*, 34-38% in *Dionaea muscipula*, and 20-25% in *S. rubra* (calculated from the diameters of cross-sections and central cylinders). Such a great proportion of central cylinder with vascular bundles in carnivorous plant roots confirms their important role for pumping mineral nutrients and water to shoots. Moreover, on the basis of a recent ecophysiological study (Adamec, 2005), carnivorous plant roots appear to be physiologically very active per unit biomass, in spite of their relatively weak proportion. Since the prevailing amount of mineral nutrients in carnivorous plants is gained by roots, the activity of which is greatly stimulated by foliar nutrient absorption from prey (Adamec, 1997, 2002), the role of roots is crucial also for carnivory.

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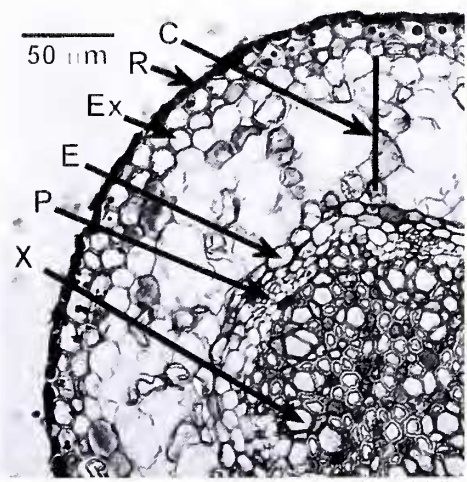

Figure 3: Cross-section through middle part of *Sarracenia rubra* root. R, rhizodermis; EX, exodermis; C, cortex; E, endodermis; P, phloem; X, xylem.

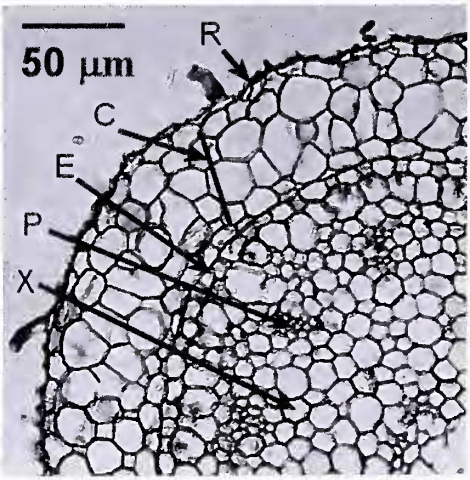

Figure 4: Cross-section through apical part (3 mm behind apex) of *Drosera adelae* root. R, rhizodermis; C, cortex; E, endodermis; P, phloem; X, xylem. All photographs by P. Kohout.